



Shallow-Water Habitats as Sources of Fallback Foods for Hominins

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1 Shallow-water habitats as sources of fallback foods for hominins.

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19 significance of fallback foods.

Abstract

Underground storage organs (USOs) have been proposed as critical fallback foods for early hominins in savanna, but there has been little discussion as to which habitats would have been important sources of USOs. USOs consumed by hominins could have included both underwater and underground storage organs, i.e. from both aquatic and terrestrial habitats. Shallow aquatic habitats tend to offer high plant growth rates, high USO densities, and relatively continuous USO availability throughout the year. Baboons in the Okavango delta use aquatic USOs as a fallback food, and aquatic or semi-aquatic USOs support high-density human populations in various parts of the world. As expected given fossilization requisites, the African early to mid Pleistocene shows an association of *Homo* and *Paranthropus* fossils with shallow-water and flooded habitats where high densities of plant-bearing USOs are likely to have occurred. Given that early hominins in the tropics lived in relatively dry habitats, while others occupied temperate latitudes, ripe, fleshy fruits of the type preferred by African apes would not normally have been available year round. We therefore suggest that water-associated USOs were likely to have been key fallback foods, and that dry-season access to aquatic habitats would have been an important predictor of hominin home range quality. This study differs from traditional savanna chimpanzee models of hominin origins by proposing that access to aquatic habitats was a necessary condition for adaptation to savanna habitats. It also raises the possibility that harvesting efficiency in shallow water promoted adaptations for habitual bipedality in early hominins.

1 Inhabiting areas with low rainfall and temperate climates, early to mid Pleistocene
2 African hominins would have needed to find plant foods year-round but would have
3 found difficulty in obtaining them during periods of low plant productivity. During some
4 periods of the annual cycle fruits tend to be unpredictable or scarce (Peters et al., 1984).
5 Nuts and seeds are often then available, but like fruits are too seasonal to be relied on
6 (Peters 1987). In savanna¹, during periods of fruit scarcity, the herbaceous foliage that
7 forest-living African apes tend to eat as a fallback is also scarce (Remis, 1997; Tutin,
8 1997; Wrangham 2005). Some primates including orangutans *Pongo pygmaeus* utilize
9 inner bark during periods of fruit shortage (Knott, 1998), and bark-eating could in theory
10 be important for savanna chimpanzees (Pruetz 2006). However extensive bark-eating has
11 not yet been recorded by chimpanzees in savanna: the density of suitable trees may be
12 insufficient outside rainforest. Meat has been proposed as a possible fallback food,
13 though Speth (1989) argued that during dry seasons the fat content of meat would have
14 been so low that protein poisoning would have been induced by a diet of more than about
15 30% meat. By contrast, plant underground storage organs (USOs) tend to be nutritionally
16 adequate and predictably available during low-growth seasons, features USOs owe to
17 their primary function of storing nutrients and/or water (Andersen, 1987; Laden and
18 Wrangham, 2005). USOs have therefore been proposed to be important components of
19 the hominin diet (Hatley and Kappelman, 1980; Brain and Shipman, 1993; O'Connell et
20 al. 1999; Wrangham et al. 1999). An increase in USO consumption may have even
21 facilitated the hypothesized hominin shift from forest to more open habitats (Laden and
22 Wrangham, 2005).

Ecological, archaeological, dental, nutritional and comparative data all support the proposed dietary importance of USOs in hominin evolution (Hatley and Kappelman, 1980; Laden and Wrangham, 2005). Edible USOs are much more abundant in savanna than rainforest habitats and there is little competition among mammals for USOs, since their underground location makes them unavailable to most species. USOs are widely eaten by human hunter-gatherers, hominid fossil sites characteristically sample habitats rich in USOs, and early hominin remains exhibit stable isotope signals with values similar to those of the USO-eating mole-rats (Bathyergidae) (Yeakel et al., 2007). Humans and early hominins all have jaws and teeth that appear well adapted for eating USOs (Hatley and Kappelman, 1980; Ungar et al., 2006). Thus Ungar et al. (2006) find that habiline teeth are adapted to crushing hard and brittle objects, while Dominy et al. (2008) conclude that USOs such as corms show low toughness but are hard and brittle. Hominin dental adaptations for processing USOs are consistent with the strong selective pressures that fallback foods are expected to place on an organism's food-processing structures (Marshall and Wrangham, 2007). USOs are a valuable human staple because they have a low concentration of fiber (Schoeninger et al., 2001; Conklin-Brittain et al., 2002) and may have sufficient nutritional quality to be significant dietary components for most human populations (Peters and Vogel, 2005; Laden and Wrangham, 2005). Finally chimpanzees have the cognitive ability to find and extract tubers using tools (Hernandez-Aguilar et al., 2007) or with their bare hands (Lanjouw, 2002), indicating that the last common ancestor of chimpanzees and humans (LCA) and early hominins probably also shared these abilities.

1 USOs are thus well-supported candidates as fallback foods for early hominins.
2 However their proposed importance in hominin evolution has been challenged. For
3 instance some USOs need to be cooked by humans to be edible, and there is little direct
4 evidence for control of fire in the Lower Paleolithic (e.g. Plummer, 2004). Furthermore,
5 the caloric value of some wild tubers is so low that their nutritional significance is
6 questionable (Schoeninger et al., 2001). In addition, micro-wear studies of early *Homo*
7 reveal fewer pits than expected for a hard-object specialist, and early *Homo* is argued to
8 have had too much occlusal relief to be well adapted to eating USOs (Ungar et al., 2006).
9 Moreover, African hunter-gatherer populations where USOs are reported to be most
10 important in the diet (Hadza and San) are believed to be “demographic sinks”. Living in
11 marginal environments, these groups export few genes outside of their population and
12 have thus been argued to be evolutionarily irrelevant (Peters and O’Brien, 1994;
13 Plummer, 2004). Against these challenges, not all USOs have low caloric value or need
14 to be cooked to be edible; USOs are not uniformly hard and brittle (Dominy et al., 2008);
15 and USOs are eaten in many different environments.

16 Resolving the importance of USOs as hominin fallback foods may be aided by
17 consideration of the mechanical and nutritional characteristics of different USO types
18 (e.g. Dominy et al., 2008), and of food productivity in different habitats, the latter of
19 which we focus on. While savannas are known to produce more edible USOs than
20 rainforests, variability in USO production among different types of savanna habitats has
21 not yet been examined in any detail. Here we propose that localized aquatic habitats
22 would have been particularly productive of USOs during seasons when preferred hominin
23 foods were scarce (cf. Wrangham, 2005). This hypothesis is in accord with evidence that

1 hominins utilized C₄ food items such as sedges (van der Merwe et al. 2008), and more
2 generally with the proposed importance of aquatic habitats as food sources based on
3 paleoecology (Copeland, 2007). It also suggests that aquatic habitats would have been a
4 valuable focus of hominin foraging during seasons of food scarcity, and that these
5 habitats would have had important implications for hominin range use and population
6 distribution. Our food-derived hypothesis thus conforms to prior suggestions that aquatic
7 habitats have been important in hominin ecology (e.g. Jolly, 1970; Verhaegen et al.,
8 2002).

9 We first examine whether plants growing in aquatic habitats tend to be especially
10 productive of USOs. We then present data on baboon (*Papio cynocephalus ursinus*) diet
11 in the Okavango Delta (Botswana) in order to test the hypothesis that a catarrhine with
12 access to shallow water habitats surrounded by relatively arid land uses aquatic USOs as
13 fallback foods. The Okavango baboon data together with data on USO ingestion in
14 modern human populations is further used to assess the hypothesis that USOs would have
15 been a likely fallback foods for hominins living in shallow water habitats. Although
16 baboon diets are not appropriate analogues for the specific composition of hominin diets
17 (Codron et al. 2008), the fact that baboons and modern humans consume USOs suggests
18 that early hominins might do so also. Finally, we review the depositional habitats of early
19 fossil hominins (i.e. *Paranthropus* and *Homo*), to test if the hominin fossil record is in
20 accord with the use of shallow water USOs as fallback foods.

21 **Are aquatic habitats especially productive of USOs?**

22 Because light and water are principal factors limiting plant growth, tropical and
23 sub-tropical shallow-water habitats tend to produce a high biomass of plant material

1 compared to terrestrial habitats (Westlake, 1982). Aquatic habitats might therefore be
2 unusually productive of USOs. Accordingly we consider USO productivity in the three
3 main macrophyte types known to grow in shallow water: (1) fully aquatic macrophytes
4 with floating leaves; (2) semi-aquatic or emergent macrophytes, i.e. plants with roots
5 anchored below water but leaves and stems largely above water; and (3) floodplain herbs,
6 which have roots submerged in water only seasonally.

7 (1) Aquatic macrophytes usually occur in still or slowly moving water. Their flat
8 floating leaves facilitate maximal absorption of incoming light and high productivity. The
9 high specific heat and low heat conductivity of water offer these plants stable thermal
10 conditions and hence a longer growing season than experienced by neighboring terrestrial
11 plants (Wetzel, 1988). Potentially, therefore, they are highly productive. They achieve
12 maximal growth in seasonally flooded or slowly moving waters, whereas in stagnant
13 swamps growth is usually reduced due to nutrient deficiency, especially low nitrogen
14 (Breen et al., 1988).

15 The most common aquatic macrophytes are water-lilies of the family
16 Nymphaeaceae. Nymphaeaceae are found worldwide and include three dominant genera,
17 i.e, white water-lilies *Nymphaea* (the main African aquatic macrophyte), yellow water-
18 lillies *Nuphar*, and water-lotuses *Nelumbo*. All produce abundant USOs that make up a
19 large proportion of plant biomass. For instance the rhizome of *Nuphar* spp. accounts for
20 about 80% of the plant's biomass (den Hartog and van der Velde, 1988). The rhizomes
21 have maximal nutrient quality at the end of the high-growth season (Brock et al., 1983).

22 USOs of *Nymphaea*, *Nuphar* and *Nelumbo* include corms, tubers and/or rhizomes,
23 all of which are eaten both raw and cooked in every continent, by both farmers and

1 hunter-gatherers (Brand-Miller et al., 1993; Jones and Meehan, 1989; Tull, 1999;
2 Chawanje et al., 2001). The USOs of *Nymphaea* appear to be fallback foods in the
3 Okavango Delta, Botswana. There the seeds, stems and USOs of *Nymphaea nouchali*
4 are eaten by at least four modern human populations. Ingestion of raw corms and stems is
5 especially common when food is scarce (Campbell, 1986; Ellery and Ellery, 1997; Roodt,
6 1998).

7 (2) Semi-aquatic or emergent macrophytes are found in shallow water along the
8 edges of lakes, rivers and streams. Prominent examples include papyrus *Cyperus*
9 *papyrus*, cattails *Typha* spp., and swamp potatoes or arrowhead *Sagittaria* spp. Like
10 aquatic macrophytes, semi-aquatic macrophytes also show very high natural productivity
11 thanks to their efficient canopies and unlimited water supply. For instance papyrus has
12 one of the highest biomass growth rates known (up to 125 metric tons dry weight per ha
13 per year, compared to 20-85 for grasslands and crops: Westlake, 1982). Like aquatic
14 plants emergent macrophytes tend to invest heavily in USOs, e.g. around half of the
15 biomass of tropical *Typha* is in USOs (Westlake, 1982). Their USO nutrient quality is
16 high (e.g. *Cyperus papyrus*, van der Merwe et al., 2008) and like water-lilies is maximal
17 during the dry (low-growth) season (Garver et al., 1988). These plants allow easy
18 harvesting because they are found in large accessible patches (e.g. *Scirpus*, *Typha*;
19 Copeland, 2007).

20 Cattails *Typha* spp., a wild semi-aquatic macrophyte, are so productive that their
21 effect on human settlement patterns can be akin to that of an agricultural crop (Mitchell,
22 1839; Gott, 1999). According to historical accounts, cattail rhizomes were a main plant
23 food, eaten year-round by aborigines inhabiting the lower Murray region of south-eastern

1 Australia (Gott, 1999). Given this rhizome's abundance in the well-watered parts of this
2 region, these hunter-gatherers enjoyed a sedentary lifestyle. At the time of European
3 contact population densities here were higher than anywhere else in Australia (Pate,
4 2006; Humphries, 2007). In fact, the population size, density and mobility was so similar
5 to that of agricultural people that the aborigines living there were subject to pathologies
6 similar to those associated with agriculture (Pate, 2006).

7 *Sagittaria* spp. also produce abundant tubers. Edible raw though preferably
8 cooked, they were a staple for North American hunter-gatherers (Richardson 1981).

9 These examples show that semi-aquatic macrophytes have a high potential for producing
10 USOs that are eaten extensively, at all times of year.

11 (3) Floodplain herbs are found in seasonally flooded areas adjacent to lakes, rivers
12 and streams. When water is available these plants store nutrients and water in USOs that
13 enable them to lie dormant through periods of low growth and re-emerge when growth is
14 once again optimal. Australian aborigines heavily exploit floodplain herbs such as corms
15 of *Cyperus rotundus* and *Eleocharis dulcis*, which they may eat raw or cooked (Isaacs,
16 1987). For instance, Tindale (1974: 97) described *C. rotundus* corms as "an important
17 standby item of diet... so widespread that there is little thought of it as being a clan
18 possession; anyone may eat at will" even though "those who feed on it for long periods
19 develop swollen bellies." Hillman et al. (1989) showed that *C. rotundus* USOs were the
20 staple food of Paleolithic hunter-gatherers along the Nile (cited by van der Merwe, 2005).
21 In the absence of agriculture, floodplain herbs can evidently be a highly productive
22 source of edible USOs.

Thus the three major types of shallow-water macrophyte include dominant plants of high natural productivity. These all produce USOs year-round, which are abundant, edible and have a high nutrient quality during dry seasons, which are times of low plant growth. The USOs of all three are recorded as plant remains in archaeological sites (e.g. *Nymphaea*, *Typha*, *Cyperus rotundus*: van der Merwe, 2005). Notably, Copeland (2007) found that herbaceous USOs from shallow-water habitats are more likely to be edible than those from drier habitats, and many can be eaten raw. All these plants can be easily located and harvested by humans. We propose, therefore, that shallow-water habitats may have served as an important source of USOs for hominins during periods of food shortage.

MATERIALS AND METHODS

As a test of whether USOs in tropical aquatic habitats are eaten as fallback foods we analyzed data on baboons in the Okavango.

Dietary data for baboons were collected from June 2006 to June 2007, from a group of 70-85 free-ranging chacma baboons (*Papio cynocephalus ursinus*) occupying about 5 sq km of the Moremi Game Reserve in the Okavango Delta of Botswana (23°02'E, 19°31'S). The study site was described by Cheney and Seyfarth (2007). It floods annually from approximately June through October, leaving only islands above water, i.e. elevated tree-lined areas ca. 1 to >100 ha in extent. Observed subjects consisted of 29-31 adult females, which were evenly sampled in 10-minute focal animal observations (Altmann, 1974; Cheney et al., 2004; Cheney & Seyfarth, 2007). Observers scored feeding activity at the end of every 10-minute focal observation, assigning foods

1 eaten to one of 33 categories. Feeding data were compiled from a total of 5365 focal
2 observations (mean 412.7 feeding records per month, SD 190.4). Foods were unidentified
3 in 3.1% of records. Data were collected primarily in the morning hours, before 1 p.m.

4 To assess which items were used as fallback foods we classified the original 33
5 categories into four major groups, i.e. Fruits, Foliage, USOs , and Other Foods. “Foliage”
6 included grass blades, and the leaf, shoots and pith of various identified and unidentified
7 herbs. “Other Foods” included insects, *Acacia* products, flowers, snails, seeds, items
8 extracted from elephant (*Loxodonta africana*) feces and various uncommon animal and
9 plant items. Feeding records for each of the four major food groups including USOs were
10 tabulated monthly as a percent of feeding records for all four major food groups. Feeding
11 records of unidentified foods were reported monthly as a percentage of total feeding
12 records (Table 1). Fallback foods were defined as those whose consumption was
13 negatively correlated with the fruit component of the diet (Marshall and Wrangham,
14 2007).

15 With respect to early hominin habitats we considered only those African hominin
16 fossil localities between 1.4 and 2.5 my old. This is the time interval in which *Homo*
17 appears (Leakey et al, 1964; Leakey, 1973; Feibel et al., 1989; Hay and Kyser, 2001),
18 many of the anatomically unique human specializations develop (Sarmiento, 1998), and
19 the East and South African climate purportedly turns drier (deMenocal and Bloemendal,
20 1995). Considering the strong commitment of the unique human anatomy (see Sarmiento,
21 1998), the selective pressures that brought it about must have occurred over a prolonged
22 period of hominin evolution and justify examining such a long history in the middle third
23 of our lineage’s geologic record. Temperature and rainfall data come from meteorological

1 records and pertain to current conditions at each fossil locality, rather than conditions
2 when fossils were deposited. Because African land mass position relative to the equator
3 and oceans would have changed only negligibly in the last 2.5 million years, and
4 relatively little mountain building in eastern and southern Africa has taken place since
5 then, it is unlikely that the climate at any locality would have been drastically different
6 than it is today.² Latitude, longitude and elevation data presented come from the literature
7 and one of the authors' notes (EES). Data are summarized in Tables 2 and 3, and in
8 Results. A review of the flora and fauna of East African alkaline lakes and South African
9 flooded grasslands and glades is included in the discussion. Because fossil deposition is
10 often dependent on water a discussion as to how taphonomy may bear on our results is
11 included.

13 RESULTS

14 The use of USOs as fallback foods by baboons.

15 Table 1 summarizes the Okavango baboon diet. The rhizomes or roots of
16 *Nymphaea nouchali* provided most of the USOs consumed, on average 79.3% of USO
17 feeding records. Baboons ate *N. nouchali* roots and rhizomes from the water's edge,
18 wading to a depth of a few centimeters to pull them from soft mud. The remaining USOs
19 in the diet included various unidentified corms, tubers and roots.

20 Fruits were the food type eaten most frequently (Table 1). If seeds were included
21 as fruits (cf. Hill and Dunbar, 2002), the monthly mean for fruit-eating rose from 37.8%
22 to 43.6%. Important fruits in the diet included those of the sausage-tree *Kigelia* sp.
23 (averaging 45.1% of fruit-records per month), a strangling fig eaten by humans as well as

1 baboons (*Ficus thoningii*, 21.0%), jackalberry (*Diospyros mespiliformis*, 17.3%), and
2 palm-nuts (*Hyphaene petersiana*, 8.0%). We assumed that fruits were a preferred food
3 because they appeared to be eaten in proportion to their availability, as was the case for
4 baboons and cercopithecines in other studies (Hill and Dunbar, 2002; Marshall and
5 Wrangham, 2007).

6 Across the months there was no significant correlation between the proportion of
7 time spent eating fruit and the proportion of time spent eating Foliage ($n = 13$ months, r^2
8 $= 0.08$, P n.s.), or Other Foods ($r^2 = 0.01$, P n.s.). Foliage and Other Foods were therefore
9 not fallback foods. By contrast, the proportion of time spent eating USOs was negatively
10 correlated with the proportion of time spent eating fruits ($n = 13$, $r^2 = 0.61$, $P < .01$; Fig.
11 1). When fruit and Foliage were combined into a single category a similar negative
12 correlation occurred with USOs ($n = 13$, $r^2 = 0.78$, $P < .0001$), but again not with Other
13 Foods ($n = 13$, $r^2 = 0.01$, P n.s.). USOs were therefore concluded to be a fallback food for
14 Okavango baboons, whereas foliage and Other Foods were not a fallback food. Foliage
15 was possibly a preferred food, since USOs were eaten more often when less foliage was
16 eaten ($n = 13$, $r^2 = 0.41$, $P < .02$).

17

18 ***** TABLE 1 AND FIGURE 1 ABOUT HERE *****

19

20 **Hominin fossil sites.**

21 Data on African hominin fossil sites are collated in Tables 2 and 3. Sites range
22 beyond tropical Africa from slightly north of 11°N to slightly beyond 26°S. Nearly all
23 hominin fossil localities have a relatively dry climate with marked rainfall seasonality

1 restricted to a single wet season. Konso, Chesowanja and Chemeron are exceptions.
2 Slightly north of the equator, Chesowanja and Chemeron may occasionally show two
3 rainfall seasons (i.e. a long and a short one) and a much wetter climate.³ Konso more
4 commonly exhibits two rainy season, but shares a relatively dry climate with the other
5 hominin fossil sites.

6 With the exception of the South African caves, most of the fossils are associated
7 with floodplain or lake margin depositional habitats reflecting lake shores or flooded
8 grasslands (Table 2). For example, the Shungura formation which shows a considerable
9 percentage of high-energy depositional habitats (i.e. rivers and stream beds) yields its
10 most complete hominins (e.g. the associated OMO 323-1976 skeleton; Alemseged, et al.
11 2002) principally in floodplains. The majority of water-lain deposits are associated with
12 alkaline lakes (8 out of 11) three of which (i.e. those pertaining to Konso, Olduvai, and
13 Peninj) were strongly alkaline at the time of deposition (Suwa et al, 2003; Hay and
14 Kyser, 2001; Lind and Morrison, 1974).

15
16 ***** TABLES 2 AND 3 ABOUT HERE *****

17
18 Fauna and flora at the majority of the fossil deposits reflect relatively dry
19 climates, but with nearby water availability. Notably, although all the South African early
20 hominin sites are cave deposits, the majority of them are in close proximity to streams or
21 flooded glades. None of the flora, fauna or current climatic variables associated with any
22 of the hominin deposits is indicative of tropical forests. Climatic, and fauna and flora data
23 indicates surrounding scrubland or grassland habitats at most fossil sites. The exceptions

are Chemeron and Chesowanja which suggest bushland and/or woodlands with a precipitation close to the lower limits necessary for forests.

Analysis of sand grain angularity and ratios of chert to quartz in breccia from Sterkfontein, Swartkrans, and Makapansgat caves suggests that these deposits were slightly drier during the time of deposition than they are today (Brain, 1958). Kromdraai B is the only exception, indicating a climate somewhat wetter than the current one, i.e. ~1000 mm of precipitation (Brain, 1958). However, the possibility of stream alluvium contaminating the Kromdraai B breccia makes this rainfall estimate uncertain. Micromammal studies of South African early hominin fossil sites confirm a slightly drier climate and presence of grasslands dating back at least to 3 my (Avery, 2001). In Shungura members G-H and Koobi Fora's Okote member the presence of desert jerboa (*Jaculus*) suggest nearby desert, barren land, or at best only scattered vegetation during the time those members were deposited. The remaining Shungura and KBS fauna further confirm a climate as dry or drier than exists there today (Feibel et al., 1991). Overall, paleoenvironmental studies are more or less in accord with current temperatures and precipitation data at each of the fossil localities.

REVIEW AND DISCUSSION

Our hypothesis that aquatic habitats produce sufficiently predictable, abundant and high-quality USOs to have provided potential fallback foods for early hominins is supported by evidence from the three major types of herbaceous macrophyte in aquatic habitats (water-lilies, semi-aquatic emergents and floodplain herbs). These three types of plant all produce large amounts of USOs edible by humans, and their USOs have high

1 nutrient quality during seasons of low growth when preferred foods are expected to be
2 scarce. Aquatic habitats once occupied by hunter-gatherers have mostly been taken over
3 by farmers, but in two cases where hunter-gatherers persisted (i.e. Botswana river peoples
4 and aborigines living at high density in south-east Australia) aquatic USOs are recorded
5 as fallback foods and staples respectively. Whether foods eaten as staples are also
6 fallback foods depends on whether their consumption correlates inversely with the
7 availability of preferred foods (Marshall and Wrangham, 2007). This means that without
8 knowing the availability of preferred foods it cannot be determined if USOs were
9 fallback foods for south-east Australian aborigines. However, the potential of non-
10 agricultural wetland habitats to be important sources of USOs is clear. The USOs could
11 be fallback foods, staples, or both.

12 Our analysis showed that Okavango baboons exploit this wetland potential.
13 Within the single baboon population examined, aquatic USOs comprised the majority of
14 USOs eaten and USOs were more abundantly eaten during months of low fruit
15 consumption. No plant or animal items other than USOs could be shown to provide our
16 baboon population with fallback foods. Our observations agree with those of previous
17 studies. Across 15 reported baboon populations USO consumption is negatively
18 correlated with fruit-eating, suggesting that baboons routinely use USOs as fallback foods
19 (Hill and Dunbar, 2002). See also Alberts et al. (2005, p. 172), who concluded that grass
20 corms were fallback foods because they “were the focus of intensive foraging activity only
21 during the dry season, when key preferred foods (notably green grass blades and fruit)
22 were scarce.”

23 Okavango is a particularly rich habitat for baboons (Johnson, 2003). Hundreds of
24 troops occupy the delta at a higher population density (17-43 individuals per sq km) than

1 recorded by Hamilton et al. (1976) for any other wild baboons (n = 10 populations).
2 Elsewhere, baboon populations vary in their use of USOs. Thus in 4 of the 15 baboon
3 populations reviewed by Hill and Dunbar (2002) USOs comprised less than 3% of the
4 annual diet. Even in the Okavango, USOs may not always act as fallback foods, given
5 that our data come from only one annual cycle. Furthermore, in tropical savannas the dry
6 season is not necessarily the period when fruits are most scarce (Pruetz, 2006). USOs,
7 therefore, are not expected to be a universal source of fallback foods. But the fact that in
8 Okavango USOs provide fallback foods for a population of baboons living at relatively
9 high densities in shallow water habitats surrounded by semiarid land with a strongly
10 seasonal climate supports the hypothesis that aquatic habitats may have had a similar
11 function for hominins living in similar conditions.

12 **East Africa alkaline lakes and the flooded grassland and glades adjacent to the** 13 **South African caves**

14 The strong association of early hominin fossils with slow moving and shallow-
15 water habitats where aquatic USOs would often have been abundant supports our
16 hypothesis that aquatic USOs could have served as fallback foods for early hominins.
17 Considering the bone preserving qualities of a high pH, it is not surprising that many of
18 the hominin fossil deposits are associated with alkaline lakes. These lakes are situated
19 along the East African rift, tend to have relatively dry climates with a single rainy season,
20 are usually shallow with very gradually descending bottoms, and are surrounded by a
21 sizable area of flat low-lying terrain that seasonally floods and dries (Ross, 1955; Feibel,
22 et al. 1991; Hay and Kyser, 2001; Carney et al, 1971; Table 2). Trees and shrubs tolerant
23 of saline soils grow at the lake margin where their roots are exposed to repeated flooding

1 and drying, such as gum myrrh (*Commiphora*), salt cedar (*Tamarix*), miswak
2 (*Salvadora*), seepweed (*Suaeda*), bush willow (*Combretum*) and willow (*Salix*). Because
3 solutes in these lakes may be highly concentrated, non-saline tolerant trees when present
4 occur mainly along the larger permanent feeding streams, which if large enough may give
5 rise to riverine forest. The latter is composed mainly of colonizing (secondary growth)
6 trees (e.g. *Albizia*, *Celtis*, *Ficus*, *Macaranga*, *Myrianthus*, *Solanum*, *Polyscias*, *Fagara*,
7 *Sterculia* etc.) with a relatively short lifespan. Doum (*Hyphaene*) and African fan palm
8 (*Borassus*) may also occur around permanent or seasonal feeding streams that flood
9 surrounding grassland in areas with high underground water-tables. Flooded during the
10 wet season, the land surrounding such lakes supports grasses, sedges, numerous herbs
11 (e.g. *Abutilon*, *Crotalaria*, *Hermannia*, *Hibiscus*, *Jasminum*, *Leonotis*, *Polygala*,
12 *Tephrosia*), and occasionally small shrubs (*Capparis*, *Tarenna*, *Grewia*, *Rhus* etc.). The
13 seasonal availability of water through flooding of what is otherwise relatively dry ground
14 creates periods of high and low growth that benefits plants with USOs (Lind and
15 Morrison, 1974).

16 In lakes that are not harshly alkaline, papyrus (*Cyperus papyrus*), other sedges
17 (e.g. *Cyperus disperma*), and cattails (*Typha*) grow densely in submerged lakeshore
18 forming reedbeds in shallow and slow moving water. These appear as a belt of vegetation
19 around the lake's perimeter and produce an abundant crop of USOs. Shallow coves
20 accumulating decaying plant material may transition over time into swamp forests
21 supporting *Raphia* and a variety of trees (e.g. *Cathormium*, *Celtis*, *Cola*, *Croton*,
22 *Garcinia*, *Grewia*, *Linociera*, *Syzygium* etc.) some of which (e.g. *Cathormium*) seldom
23 grow outside of swamps. Very highly alkaline lakes (e.g. Magadi, Manyara, Natron,

1 Eyasi etc.) are devoid of dense cattail and papyrus growth around their perimeter, at best
2 showing only specialized sedges growing thinly at water's edge. Probably they would not
3 have provided as rich a source of USOs as less alkaline lakes.

4 In lakes that are not excessively alkaline and support reedbeds, fusiform-shaped
5 rope fish (*Polypterus*), African arowanas (*Heterotis*), African knifefish (*Gymnarchus*
6 *niloticus*) and a number of catfish (*Clarias*, *Auchenoglanis*) (all with the ability to breathe
7 air) inhabit the still, murky water.⁴ Found throughout such lakes, adult carps (*Labeo*),
8 catfish (*Bargus*) and Nile perch (*Lates*) are more common in the deeper water, but as fry
9 they are found principally in the reedbeds. The latter form a nursery for many lake fish.
10 Otherwise, such lakes are habitat to a number of fish that have evolved reproductive and
11 migratory strategies for colonizing flooded terrain (e.g. *Alestes*, *Barbus*, *Hydrocynus*,
12 *Hyperopisus* etc.). Spiny soft-shelled turtles (*Trionyx*) and terrapins (*Pelusios*) burrow in
13 the muddy bottoms. Hippos (*Hippopotamus*) inhabit the reed beds around the lake
14 margin. Crocodiles feed and hunt in the water, using the shoreline for rest and shelter.
15 The seasonally flooded grassland surrounding lakes provide graze for white rhinoceros
16 (*Ceratotherium*), cape buffalo (*Syncerus*), water-loving antelopes (*Kobus*, *Kob*, and
17 *Tragelaphus spekei*) and rodents (*Thryonomys*). Hundreds of species of birds also use
18 alkaline lakes for food and shelter. Increased alkalinity directly curtails the variety of
19 plants and animals each lake supports and the food that would have been available to
20 hominins. Even the most alkaline lakes (Magadi and Natron), however, may support fish
21 (e.g. *Tilapia*) and invertebrates, the latter of which some birds are specialized to feed on
22 (e.g. flamingos *Phoenicopterus*). All of the flora and fauna listed above may be found in
23 the early hominin fossil deposits of alkaline lakes and a large part may have served the

1 diet of hominins throughout the time they occupied these areas. The variety of life-forms
2 attests to the richness of lake-shore, shallow-water habitat, an effect based in large part on
3 USO-bearing macrophytes. Prior to hominin emphasis on hunting and fishing these
4 shallow-water habitats would have provided abundant USOs during times of food
5 shortage, and afforded a foothold in shallow-water habitats for the subsequent
6 development of hunting and fishing techniques.

7 As noted, all the South African early hominin cave sites are associated with
8 glades or flooded terrain. Swartkrans, the site with the densest accumulation of hominins
9 (Watson, 1993a) is about 200 m west and above a meander in the Blaaubank (Rietspruit)
10 river that floods approximately 5 hectares of its valley during the rainy season supporting
11 *Typha* and promoting dense grass growth (Fig. 2). East of Swartkrans, Sterkfontein is
12 about 700 m from this glade. Downstream, Kromdraai is 500 m south of an even larger
13 patch of seasonally flooded land (the downstream continuation of the flooded land
14 adjacent to Swartkrans). Drimolen at slightly higher elevations is about 400 meters from
15 a one-hectare glade supporting tall grasses. Gladysvale, likewise, is proximal to an
16 oxbow in a stream (Skeerpoort river) that at one time may have entered the cave.
17 Makapansgat is between numerous streams that flood small patches of grassland where
18 the streams meander and converge. Situated in river valleys, the flooded land is rich with
19 organic peat and stream alluvium. Even in the dry season, when crossing these areas a
20 person may sink in mud knee-high or higher.

21 **** FIGURE 2 ABOUT HERE ****

22 Like the edaphic grasslands surrounding alkaline lakes, the South African glades
23 are seasonal with water levels and grass growth peaking in the wet season. Strong rain

1 and temperature seasonality compounded by occasional freezing temperatures in the
2 months of July-September promotes growth of plants with USOs. Submerged soil
3 supports a dense growth of cattails and a large variety of grasses and herbs including
4 members of the *Liliaceae* family. The latter produce large edible tubers which have been
5 proposed as early hominin food (Brain and Shipman, 1993). High altitudes, cold winters,
6 long dry seasons and bush fires are strong deterrents to tree growth, so transitions to
7 swamp woodlands are not as common as they are in tropical climates. Although human
8 populations have long ago extirpated most endemic large mammals that occurred at the
9 South African hominin localities, in nearby game-farms with similar terrain these glades
10 are always sites of animal aggregation, especially in the dry season.⁵ They attract more or
11 less the same mammalian genera found along the shores of East African alkaline lakes.
12 Although the exact size of the South African glades during the time *Paranthropus* and
13 early *Homo* inhabited the South African sites still needs to be worked out, dolomite
14 faulting and terrain contours leaves no doubt that these glades existed during fossil
15 deposition.

16 As in East Africa, in South Africa early hominins would have endured long dry
17 seasons within range of shallow-water habitats with abundant USO production. The low
18 food productivity of non-watered land during the dry season in both East and South
19 African habitats supports the likelihood that nearby shallow-water habitats with abundant
20 food production would have been used by hominins, and USOs would have served as a
21 fallback food especially prior to hominins emphasizing hunting and fishing. The location
22 of early hominin fossil remains and the nearly complete preservation of many fragile

skeletal parts during deposition leaves no doubt that shallow-water habitats would have been part of the hominin range.

Hominin habitat preferences, bipedality, wading and the fossil record

The evidence that hominins ranged into shallow-water habitats and may have used USOs as fallback foods raises questions as to how hominins would have harvested USOs. We suggest that emphasis on USOs could have favored bipedal wading. Specifically, we propose that: (1) the LCA (last common ancestor of humans and *Pan*) and the earliest hominins could have waded bipedally rather than quadrupedally to collect aquatic USOs and other edible parts of aquatic and semi-aquatic macrophytes; (2) bipedal wading gave significantly increased access to these fallback foods; (3) foraging while wading bipedally would have prolonged the duration of bipedal bouts; and (4) as a result, wading could have helped select for fulltime bipedal adaptations. We assume that such a process would have been part of the origin of the hominins.

Admittedly using the fossil record to infer past behaviors and habitat preferences is fraught with difficulties. Fossilization and deposition are often associated with water so that consistently finding fossil ancestors in lake shore, mudflats, everglades, swamplands, deltas, floodplains or river bend habitats does not prove that these ancestors ate USOs, practiced wading behaviors, or would have preferentially inhabited these areas. In fact shallow-water habitats are also sites of low energy deposition, and with some exceptions are mainly the deposit types where vertebrate fossil preservation is complete enough to allow for certain identification. Because the likelihood an animal will be fossilized decreases with increases in its distance to the deposition site, fossil density ratios of our ancestors compared to those of animals with known habitat preferences from the same

1 deposits may divulge relative distances from the deposition habitat and whether our
2 ancestors commonly ranged into and exploited these habitats. Unfortunately, fossil
3 collection is usually a biased endeavor and actual representative ratios of animals at any
4 one deposit are not commonly known (Bobe et al, 2002). Moreover, hominoids typically
5 occur at relatively low densities (Sarmiento, 2003) so that density estimates based on
6 fossil finds may have a large degree of error, and comparisons of density ratios for habitat
7 preference are unlikely to yield statistically significant results.

8 Further complicating matters a generalized ape may be expected to range into a
9 wide variety of habitats including shallow-water habitats. Finding fossils of generalized
10 apes in either wading or non-wading habitats would not show whether they underwent
11 selective pressures for wading or preferentially consumed foods found in these habitats.

12 Nevertheless, the circumstantial evidence for hominins having been committed to
13 lake-margin, flooded grassland and/or glade resources in the arid areas they inhabited is
14 strong considering that 1) even in those depositional habitats where fossilization is not
15 dependent on standing water (i.e. South African caves) flooded grasslands and glades can
16 always be found nearby the deposits, and 2) prior to the appearance of the Homininae
17 such habitats are practically devoid of hominoids of any kind, but with the appearance of
18 Homininae only hominin fossils but no other hominoids are consistently found there.
19 Given the strength of this evidence, therefore, it is relevant to ask how hominins would
20 have obtained aquatic USOs. We suggest that in these habitats, hominins would have
21 been prone to bipedal wading behaviors given their great ape heritage and climbing
22 ancestry (Sarmiento, 1995, 1998).

1 Feeding behaviors seem to be the most logical choice to explain habitual
2 bipedality, since in primates feeding behaviors are known to force postures that over time
3 shape the animal's movements (Prost, 1965; Rose 1974). The most commonly accepted
4 and often cited behavior in this respect is terrestrial feeding from lower tree limbs and/or
5 around large shrubs (Rose, 1976; Wrangham, 1980; Hunt, 1994). Evidence for the unique
6 importance of such low-standing plants as sources of food, especially during seasons of
7 food scarcity when selective consequences are expected to be particularly intense, has yet
8 to be found.

9 Foraging and feeding in swamps, flooded grasslands, lake-shores or glades in
10 habitats where food is otherwise scarce offers an alternative hypothesis why habitual
11 bipedality would have been adopted. Baboons, chimpanzees, gorillas and orang-utans
12 wade in water if necessary, and great apes characteristically do so bipedally (Hornaday.
13 1910; Kortlandt, 1995; Niemitz, 2002). Bipedal wading provides access to deeper water
14 and deeper USOs that would otherwise be unreachable (Fig. 3). Moreover, keeping more
15 of the body above water as is done during bipedal wading reduces the cooling effect of
16 water enabling animals to endure colder water for longer periods. Foraging in waist-high
17 water or higher could have selected for prolonged bipedal behaviors. On the one hand,
18 once the individual is foraging in water at this depth it can no longer breathe if it reverts
19 to quadrupedal postures, and must walk bipedally to shallower areas to be able to effect
20 such postures and hold its head above water. On the other hand, most visible food would
21 be at the water surface or above and USOs could be easily attainable by pulling on the
22 emergent parts of the plants. Wading in very deep waters would not necessarily sacrifice
23 USO collection. When foraging for *Sagittaria* Native Americans were sometimes

1 observed to wade up to their necks using their feet to release tubers from the stem (Lewis,
2 1961). The tubers floated to the surface and could then be collected. Similar foraging
3 styles, with the use of feet to dislodge USOs, could also have been important for early
4 hominins foraging in deeper water. The significance of aquatic USOs for hominins could
5 therefore extend beyond being a critical food source during periods of nutritional stress.
6 As they have in other primates, fallback foods may be expected to have placed strong
7 selective pressures on early hominins. These may be directed not only at the jaws and
8 teeth, but also at the locomotor and postural adaptations (i.e bipedality) which facilitate
9 USO collection.

10 ***** FIGURE 3 ABOUT HERE *****

11 12 **Implications for models of hominization.**

13 Our review shows that early fossil hominins are almost always associated with
14 aquatic or flooded habitats and strongly seasonal climates with periods of relatively low
15 rainfall. *Homo*, *Paranthropus* and their common ancestor, therefore, are likely to have
16 gravitated towards shallow water habitats during dry seasons in search of food. Here they
17 would have had regular access to aquatic USOs.

18 We suggest that a similar access may have applied to earlier australopithecines
19 and other members of the hominoid stock. In fact, many of the very earliest unambiguous
20 hominoid fossils (i.e. *Oreopithecus*, *Sahelanthropus* and *Dryopithecus*), and other fossils
21 claimed to be members of our lineage (*Orrorin*, *Ardipithecus*, *Australopithecus*
22 *annamensis*, *A. afarensis* and *A. africanus*) all come from depositional habitats
23 representing swamp forests, lake shores, or seasonally flooded grasslands or were found

1 close to such shallow-water habitats (this study; Hurzeler, 1958; Vignaud et al., 2002;
2 Kazmer, 1990; Wynn, 2000; Pickford and Senut, 2001; WoldeGabriel et al., 2001;
3 Bonnefille et al., 2004).

4 Considering the wading behaviors of living chimpanzees, bonobos and gorillas
5 (Kortlandt, 1995, Niemitz, 2002), it is likely that prior to human divergence the common
6 human African ape ancestor waded bipedally and used shallow-water habitats
7 opportunistically (Fig. 3). With hominin divergence and shifts to more open habitats
8 commitment to shallow-water habitats increased to the point of dependency in the driest
9 habitats.

10 Our analysis suggests that aquatic habitats would have predictably provided USOs
11 as fallback foods for early hominins when food was scarce in the surrounding grasslands
12 and scrublands. This idea conforms to Copeland's (2007) reconstruction of habitats in
13 Bed II of the Olduvai Gorge, indicating that river-side habitats were important sources of
14 food. It also conforms to the conclusion that a strong C₄ signal found regularly in
15 hominins (including *Australopithecus*, *Paranthropus* and *Homo*) comes partly from wet-
16 land sedges Cyperaceae (Sponheimer et al., 2005; van der Merwe, 2005; van der Merwe
17 et al., 2008).

18 The possibility that sedges were responsible for the C₄ signal in hominins is
19 admittedly debatable. It has been argued (Sponheimer et al., 2005) that aquatic habitats
20 may have been too rare in South Africa to be important sources of sedge foods. We agree
21 that aquatic habitats in South Africa were probably as rare during early hominin times as
22 they are today. Hominin home ranges, however, would have covered a mosaic of habitats
23 including aquatic ones (Copeland, 2007). Within the latter, we suggest that hominins

1 would have heavily exploited shallow-water habitats, i.e. the edges of slowly moving
2 rivers, deltas, marshes, glades and lakes. Different social groups and populations would
3 have differed in their access to such aquatic habitats. Those with greater access would be
4 expected to have survived better in dry seasons and times of food scarcity, presumably at
5 higher population density, than those with less. We suggest that the best home ranges
6 would have been those that included sufficient aquatic habitat to provide adequate
7 fallback USOs during times of food scarcity.

8 How early hominins made the ecological shift to open habitats is an unsolved
9 problem. The savanna chimpanzee model is a much discussed ecological solution. It
10 suggests that the first hominins originated when they successfully occupied dry savannas
11 on the fringes of the equatorial rainforest, a habitat-shift which has been more recently
12 repeated by some modern chimpanzee populations (Moore, 1996; Hunt and McGrew,
13 2002; Hernandez-Aguilar et al., 2007). It argues that adaptation to these arid habitats
14 occurred partly through behavioral innovations such as the use of digging tools, hunting
15 weapons and new thermo-regulatory strategies (Hernandez-Aguilar et al., 2007; Pruetz
16 and Bertolani, 2007; Pruetz, 2007). It also implies that the foods and habitats exploited by
17 early hominins were similar to those used by dry-country chimpanzees.

18 In contrast to the savanna chimpanzee model, an aquatic-habitat scenario suggests
19 that the LCA and/or early hominins made the shift to more open arid areas as a result of
20 being able to exploit areas of shallow water that were not necessarily close to riverine
21 forests or rainforest fringes (Wrangham 2005). The ability to reach such habitats may
22 have depended on unusual biogeographical events. Once there, we propose, hominin
23 ancestors were able to flourish partly by exploiting a new suite of foods, including

1 underwater USOs. This aquatic-habitat scenario conforms to the notion advanced by
2 Sponheimer and Lee-Thorp (2003), based on stable isotope data, that hominins and forest
3 apes would have eaten different foods even if their ranges overlapped. Our analysis thus
4 suggests that hominins exploiting aquatic USOs, something neither chimpanzees nor
5 gorillas are known to routinely do, would have relied importantly in seasonal habitats on
6 access to this novel food supply.

7

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16

1 **Footnotes.**

2
3 ¹ Following Laden and Wrangham (2005), we use ‘savanna’ to mean all habitats other
4 than rainforest. Savanna thus includes not only closed canopy woodlands, bush, grassland
5 etc. but also shallow-water habitats such as lake shores, deltas and the outside bends of
6 slow-moving rivers. [LOCATION OF FOOTNOTE: p. 3, line 6: “In savanna”]

7 ² Even during glacial periods areas within 30 degrees latitude of the Equator have never
8 been shown to undergo drastically lower temperatures. [LOCATION OF FOOTNOTE: p.
9 11, line 21: “than it is today”]

10 ³ Theoretically sites close to the equator should show two rainy seasons with one of the
11 two seasons (winter rains) getting progressively shorter so as to virtually disappear at 6°-
12 10° latitudinal distance north or south of the equator. However, the aridity of the East
13 African climate is such that many East African sites even those very close to the equator
14 (i.e. Peninj, Olduvai, Chesowanja and Chemeron) fail to consistently show two rainy
15 seasons (Norton-Griffiths et al., 1975, Bonnefille and Riollet, 1987, and Table 3).

16 [LOCATION OF FOOTNOTE: p. 13, line 17: “a much wetter climate”]

17 ⁴ *Protopterus* the lungfish may also inhabit reedbeds and dig into muddy lake shores, but
18 is highly sensitive to alkalinity and is not usually found in alkaline lakes. [LOCATION
19 OF FOOTNOTE: p. 18, line 16: “in the lake’s reedbeds.”]

20 ⁵ Gladysvale for instance occurs on a game farm in which such glades attract baboons,
21 antelopes and leopards. [LOCATION OF FOOTNOTE: p. 20, line 19: “game-farms with
22 similar terrain”]

1 Figure legends.

2

3 Figure 1.

4 Monthly feeding records of underground storage organs (USOs) and fruits
5 consumed by Okavango baboons, June 2006 to June 2007. Pearson correlation coefficient
6 $r = 0.78$, $n = 13$ months, $P = 0.002$.

7

8 Figure 2.

9 Aerial view of Swartkrans caves. Photo from Google Earth showing distance
10 between Swartkrans (circled in white) and the plain of the Rietspruit (outlined in white).
11 Glades show as light patches of green on either side of the stream. The white roofs, seen
12 on the lower right of photo, mark the approximate locality of the Sterkfontein site.

13 Aerial view of Swartkrans caves (circled in white) and nearby glades associated with
14 the Reitspruit stream (outlined in white). The white roofs seen on the lower right are part of
15 the Sterkfontein building complex. Sterkfontein caves are approximately 150m to the east
16 outside of the picture. Photograph taken from Google Earth.

17

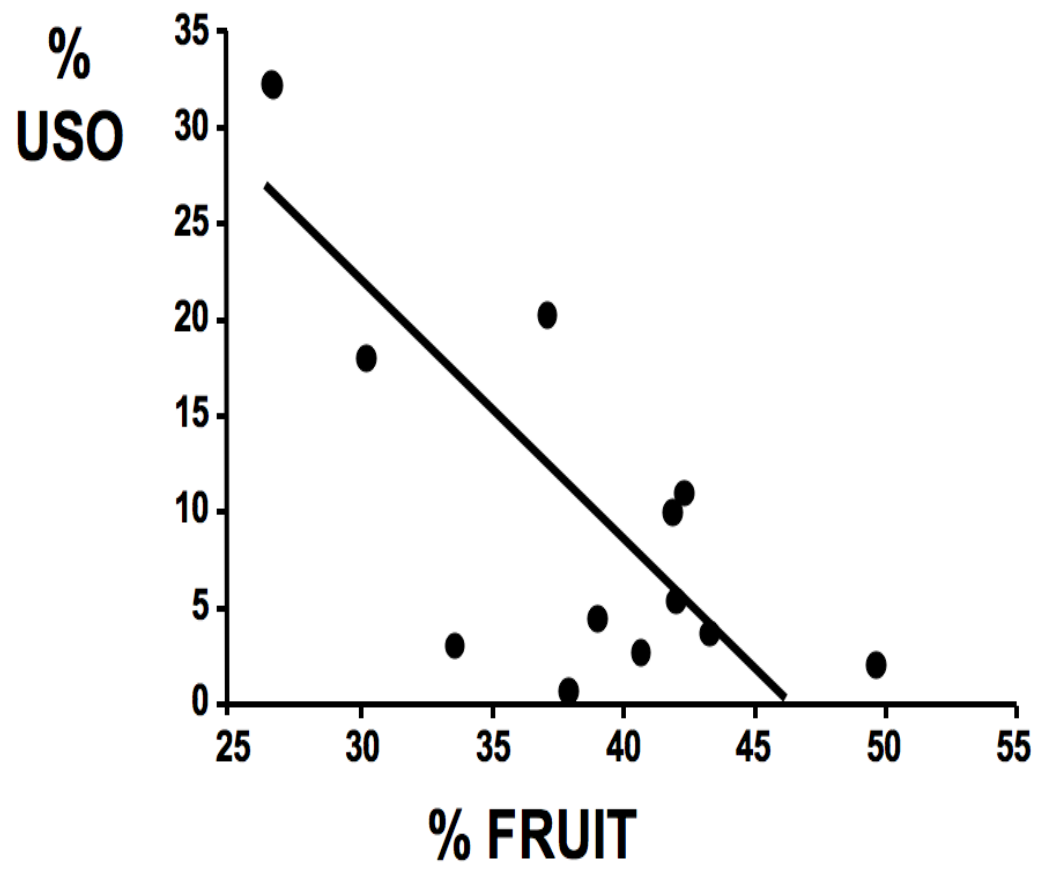
18 Figure 3.

19 Bonobo wading bipedally at Lola ya Bonobo, Democratic Republic of the Congo (©
20 Vanessa Woods). In this sanctuary for bonobos orphaned by the bushmeat trade, bonobos
21 wade up to their shoulders to obtain stems of Nymphaeaceae as food.

22

1 Fig. 1

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1 Fig. 2



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1 Fig. 3

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